KLEPTOPARASITIC BEHAVIOUR OF *ONTHOPHAGUS SUTURALIS* PERINGUEY (COLEOPTERA: SCARABAEIDAE) AND OTHER DUNG-BEETLES.

P. M. Hammond

Department of Entomology, British Museum (Natural History)
London, England SW7 5BD

Utilisation by small dung-beetles of brood material gathered by larger species has been reported by several authors. Records relating to the dung-balls of Scarabaeinae have been summarised by Halffter & Matthews (1966) and those relating to the brood supplies of Geotrupidae by Howden (1955). In the present note attention is drawn to these and other previously recorded instances of apparently kleptoparasitic behaviour by dung-feeding beetles. Some new observations are also placed on record and the possible advantages of kleptoparasitism to dung-beetles, particularly under certain environmental conditions, are discussed.

Most records of kleptoparasitic behaviour in dung-beetles relate to Aphodiinae or relatively small Scarabaeinae utilising brood or other material of larger species. More than a century ago, fairly detailed observations were made on *Aphodius porcus* (Fabricius) in Britain by Chapman (1869, 1870). Chapman's observations demonstrated that females of *A. porcus* would enter the egg chambers of *Geotrupes stercorarius* (L.), where they laid up to 10 eggs. Of 29 *Geotrupes* tunnels examined by Chapman (1869), each with 6 to 8 transverse egg chambers at a depth of between 6 and 12 inches, 8 had been visited by *A. porcus*, and a further 6 contained *A. porcus* still at work. *A. porcus* is rather infrequently found above ground in Britain and other observations suggest that this species regularly uses *Geotrupes* burrows and may be dependent on them. Sopp (1898) recorded the presence of another species, *Aphodius testudinarius* (Fabricius), in burrows of *Geotrupes mutator* (Marsham) in Britain. In this instance adults of the *Aphodius* were found in *Geotrupes* burrows during January and February, but were common above ground in dung towards the end of March, when they were *not* to be found in burrows. As *A. testudinarius* probably overwinters in the adult stage, *Geotrupes* burrows may be employed as suitable hibernation sites. If this species does utilise *Geotrupes* egg chambers for oviposition it would seem likely that such behaviour is facultative.

Other recorded instances of utilisation by *Aphodius* species of brood material gathered by larger dung-beetles, relate to the dung-balls of members of the subfamily Scarabaeinae. These cases, all noted by Halffter & Matthews (1966) or Howden (1955), include utilisation of *Scarabaeus sacer* L. balls by *Aphodius* species in France (Fabre 1897), *S. sacer* and *Copris hispanus* L. by *Aphodius* species (and also by Staphylinidae) at Tashkent (Siyazov 1913), *Phanaeus* (probably *igneus floridanus* d'Olsoufieff) by *Aphodius rubeolus* Beauvois in Florida (Howden 1955), and *Onthophagus medorensis* Brown by *Aphodius lividus* (Olivier) in Texas (Howden 1955).

Utilisation of brood material gathered by Scarabaeinae by other, generally much smaller, Scarabaeinae has also been noted for several species. Péringuey (1901, p. 171) records the observations, in Southern Africa, of G.A.K. Marshall, who informed him that "several species, notably *Onthophagus suturalis* and *Onthophagus brevicornis*, utilise the balls made by *Scarabaeus*, & c., penetrating into them while being made. In a ball of *Scarabaeus nigroaeneus* he took no less than twenty examples of *Onthophagus suturalis*." Several other species of Coprini were recorded from dung-balls of *Scarabaeus gangeticus* Laporte in Ceylon by Arrow (1931), including *Caccobius aterrimus* (Fabricius), *C. rufipennis* (Motschulsky), *Onthophagus cryptogenus* Boucomont, *O. ochreatus* d'Orbigny, and *O. pusillus* (Fabricius). Further records are those for what is probably referable to *Caccobius schreberi* (L.) in the balls of *Scarabaeus sacer* L. (Fabre 1897), *Pedaria geminata* (M'Leay) in dung-balls of other Scarabaeinae in Australia (Lea 1923), *Trichillum externepunctatum* Preudhomme in balls of *Dichotomius bosqui* (Pereira) in Argentina (Martinez 1959), *Onthophagus chevrolati* Harold in balls of *Copris armatus* Harold in Mexico (Halffter 1959), *O. suturellus* Brullé in balls of *Gymnopleurus* species (Kolenati 1846), and *O. hofneri* Harold in balls of *Canthon imitator* Brown in Arizona (Young 1969).

All of the specific instances noted above relate to occurrences of relatively small Scarabaeidae, of the subfamilies Aphodiinae or Scarabaeinae (Onthophagini or Coprini) in brood material of larger Scarabaeidae (mostly Scarabaeini, some Coprini) or Geotrupidae. However, it is likely that this type of behaviour is by no means confined to the Scarabaeidae. Several records of dung-feeding species of Diptera from buried brood-balls of Scarabaeidae are noted by Halffter & Matthews (1966), including cases where the Diptera appear to depend on this source of material for oviposition. A number of species of Oxytelinae (Staphylinidae) are also likely to be dung-feeders, both adults and larvae (Hammond, in press), and may construct brood-chambers within dung lying on the soil surface. G. B. Monteith (personal communication) has noted an association between various Staphylinidae and the "nests" of *Cephalodesmius* species in Australia. In particular, individuals of one species of *Anotylus*, which proves to be undescribed (Hammond, unpublished work), have been observed riding on the backs of *Cephalodesmius*, as well as being found in numbers in their buried brood material.

My own observations relate to species of *Onthophagus* collected during the course of the British Museum (Natural History) Entomological Expedition to South-Western Africa 1971-1972. During the course of this expedition samples of herbivorous mammal dung were collected at more than 50 sites in Angola, Botswana, South Africa, and South-West Africa, but no special attempt was made to collect the larger scarabaeoid beetles, or to make observations on the biology of species collected. However, at a locality near the Etosha Pan in South-West Africa an individual of *Scarabaeus nigroaeneus* Boheman was found in the process of rolling a dung-ball, which was collected along with the beetle. The ball was kept in a tightly-stoppered glass jar and some 3 weeks later 2 adults of *Onthophagus suturalis* Péringuey were found to have emerged from it. After a further interval of about 1 week the dung-ball was dissected but was found to contain no further beetle larvae or adults, either of *Scarabaeus* or *Onthophagus*.

Near Sesriem, on the eastern edge of the Namib Desert in South-West Africa, several individuals of the endemic *Scarabaeus rubripennis* Boheman were observed in flight over a system of fairly large dunes. Two specimens were collected from the ground where they were gathering fragments of Gemsbok dung. When found, one of the *Scarabaeus* was carrying an individual of an *Onthophagus* species on its back. The second *Scarabaeus* was seen to land on the ground and, shortly after observation of its dung-gathering activities had commenced, it was joined by an *Onthophagus* which appeared to follow it. Both individuals of the *Onthophagus* apparently belong to the same species. Later attempts to identify the Sesriem *Onthophagus* met with no success, and it is likely that the species, superficially resembling *O. ochreatus* d'Orbigny (from Arabia, North Africa, etc.), remains undescribed.

Although by no means all of the observations noted above are necessarily indicative of kleptoparasitic habits in the dung-beetles concerned, it is likely that utilisation by small dung-beetles of brood or other material gathered by larger species is widespread. Accidental inclusion of other insect species, especially their eggs, in dung buried by large Scarabaeoidea may be relatively frequent, but is clearly not always responsible for the presence of other species in such material. Observations suggest that some species seek out the brood material of large dung-beetles in which to oviposit. The absence of any specific records of predatory dung-inhabiting species (large Staphylinidae, Histeridae, etc.) from scarabaeoid dung-balls may also indicate that the eggs of dung-frequenting species are not often accidentally included in brood material which is later buried.

In some instances the use of buried brood material by adults or larvae of other species may be facultative. In other cases brood chambers may merely provide suitable hibernation or aestivation sites, especially for non-burrowing species. Use may also be made of abandoned brood material as a food source. The presence of an individual of *Onthophagus hofneri* in an abandoned, unburied *Canthon* brood-ball was interpreted by Young (1969) as an example of "eco-system economy", that is the smaller dung-beetle was utilising a convenient food-source which might otherwise have remained unexploited as food for dung-beetles or other insects. However, to be sure that this instance is not indicative of kleptoparasitic behaviour, further data concerning the oviposition behaviour of the *Onthophagus* species and its presence or absence from dung-balls which *are* buried are required.

Where buried brood material is utilised as food for adults or larvae of smaller species the fate of the "host" species' brood may vary. The eggs of the host may be eaten or killed (e.g. *Aphodius porcus*), or host larvae may starve because of depletion of the food store before they hatch. In other cases, where the "kleptoparasites" are particularly small, the host larvae may be little affected. The advantages of exploiting the buried brood material of large scarabaeoids may be several for smaller species. In the absence of competitors and predators buried dung may provide a particularly secure food supply and suitable site for oviposition. Buried dung is also considerably more protected from the vicissitudes of the climate than that above ground. Even in cool temperate regions fluctuations in temperature and humidity of dung above ground are considerable (see Landin 1961). Dessication, especially in exposed situations and in "non-crusting" dung (e.g. that of horses, sheep, etc.), may be rapid. The much greater speeds at which dung dries out in less temperate regions is documented by Hafez (1939), on the basis of studies in Egypt. The predominance of dung-*burying* species in hot and arid regions is, no doubt, associated with the prevailing rapid dessication of their food material on the surface. The life-cycles of small dung-inhabiting species are generally of short duration in the arid Tropics (Hammond, in press). However, the period necessary for the larval development of "medium-sized" species (e.g. *Onthophagus*) is likely to be longer. Brood-chambers constructed immediately beneath dung lying on the surface or brood material in relatively shallow burrows may be insufficiently protected from the rigours of the climate. In extremely arid regions the only herbivorous mammal dung available is likely to be of the non-crusting variety, generally in fairly small pellets. In such circumstances dessication of dung is so rapid that it may only be successfully exploited as brood material by those dung-beetles able to collect and bury it deeply before dessication is advanced. Some large tropical species (e.g. of *Scarabaeus)* bury brood material up to 8 feet below the surface (Arrow 1931). Such dung-balls may also be sealed, for example by a mud coating, and effectively protected from dessiccation. Small species utilising such balls as brood material for their own larvae must enter the dung-ball and oviposit before it is completed and buried. Observations noted above suggest that some *Onthophagus* species may be successful in doing this. Development of such specialised behaviour may be particularly likely to lead to obligate kleptoparasitism. It may be no coincidence that several of the observations of apparently kleptoparasitic behaviour noted here relate to dung-feeding beetles in areas where humidity is low and temperatures generally high. In such regions the brood chambers of large scarabaeoids provide a favourable niche for larval development of smaller species, a niche which may be otherwise scarce or absent.

My thanks are due to M. I. Russell for pointing out the reference to *Onthophagus suturalis*, etc. in Péringuey's (1901) classic work, and to G. B. Monteith for information concerning the habits of the Australian *Anotylus*.

REFERENCES

ARROW, G. J. 1931. The fauna of British India, including Ceylon and Burma. Coleoptera, Lamellicornia, 3 (Copridae). Taylor & Francis, London. xii + 428 p., 61 figs., 13 pls.

CHAPMAN, T. A. 1869. *Aphodius porcus*, a cuckoo parasite on *Geotrupes stercorarius*. Ent. Mon. Mag. 5:273-276.

CHAPMAN, T. A. 1870. Further note on the parasitism of *Aphodius porcus*. Ent. Mon. Mag. 6:230-231.

FABRE, J. H. 1897. Souvenirs Entomologiques, 5. 355 p.

HAFEZ, M. 1939. Some ecological observations on the insect-fauna of dung. Bull. Soc. Found. Ent. 23:241-287.

HALFFTER, G. 1959. Etologia y paleontologia de Scarabaeinae. Ciencia Mex. 19 (8-10):165-178.

HALFFTER, G. AND MATTHEWS, E. G. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Ent. Mex. 12-14:1-312.

HAMMOND, P. M. in press. A review of the genus *Anotylus* C. G. Thomson (Coleoptera: Staphylinidae). Bull. Br. Mus. Nat. Hist. (Ent.).

HOWDEN, H. F. 1955. Cases of interspecific parasitism in Scarabaeidae. J. Tenn. Acad. Sci. 30 (1):64-66.

KOLENATI, F. A. 1846. Meletemata entomologica, 5. 170 p., pls. 17-19. Petropoli.

LANDIN, B. O. 1961. Ecological studies of dung-beetles. Opusc. Ent. Supplementum 19:1-227.

LEA, A. M. 1923. Australian dung beetles of the sub-family Coprides. Rec. S. Aust. Mus. 2:353-396, pls. 6-9.

MARTINEZ, A. 1959. Catálogo de los Scarabaeidae argentinos (Coleoptera). Revta Mus. argent. Cienc. Nat. Bernardino Rivadavia Inst. Nac. Cienc. Nat. 5 (1):1-126, 4 pls.

PÉRINGUEY, L. 1901. Descriptive catalogue of the Coleoptera of South Africa (Lucanidae and Scarabaeidae) (part). Trans. S. Afr. Phil. Soc. 12:1-563.

SIYAZOV, M. M. 1913. [in Russian] Contribution a la biologie des coprophages (Coleoptera, Scarabaeidae). Russk. Ent. Obozr. 13:113-131.

SOPP, E. J. 1898. Habits of *Heptaulacus testudinarius*. Ent. Mon. Mag. 34: 114-115.

YOUNG, R. M. 1969. Ecosystem economy: *Onthophagus* using a *Canthon* brood ball. Coleop. Bull. 23 (1):24-25.

* * *

EDITORIAL–COLLECTING BEETLES IN EXOTIC PLACES WITHOUT LEAVING HOME: THE HERBARIUM[1]

John Colburn Bridwell (1932, J. New York Bot. Garden 33:105-109) long ago published a note on collecting beetles, especially bruchids, in herbaria. This technique needs to be re-emphasized, as a means for gathering much needed complementary data on poorly known groups.

Many bruchids and weevils, and some other groups of Coleoptera and certain other insect groups, leave not only traces of their activity on herbarium specimens but may themselves still be present. Among beetles that attack fruits and flower buds, some leave the food source to pupate in the ground, hence leaving little or no useful, recoverable trace on the herbarium specimen. Others, however, pupate *in situ*; and it is for these that I have found the herbarium a useful—and much neglected—resource.

Recognition. Generally, a distinctive exit hole is prepared, either by larva or adult, before emergence. Frequently, for some reason, the adult has not yet emerged; it may have been physiologically unable to do so, or it may have been trapped during preparation of the plant specimen. In general, unless seeking expected clues, I scan the herbarium sheets quickly; thus, when I do find an infested plant specimen, it is likely to be heavily infested and therefore contain several individuals including fully developed adult males (the most valuable for taxonomic purposes).

Occasionally, plant specimens may be found with emergence holes but no visible beetles, yet specimens are badly needed. In such instances, as with legumes, it may be possible to find infested seeds containing unemerged adults by pinching the apparently intact seeds, or it may be possible to detect seeds containing beetles because of thinned, discolored patches on the seed coat.

---

[1] Work carried out under support of D. H. Janzen's NSF Grants GB35032X and BMS 75-14268.